

Taxonomy, vocalisations and natural history of *Philydor dimidiatum* (Furnariidae), with comments on the systematics of *Syndactyla* and *Simoxenops*

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Because of the inherited nature of vocalisations within the suboscines (Lanyon 1978, Kroodsma 1984, 1989), vocalisations are often a strong indication of relationships within this group. In the Neotropical family Furnariidae, vocalisations in concert with morphological and behavioural aspects have been used to elucidate relationships at the species and generic level (Parker *et al.* 1985, Whitney & Pacheco 1994, Kratter & Parker 1997, Zimmer 1997, 2002, Remsen 2003). In fact, Vaurie's (1971, 1980) systematic revisions of this family, which did not include vocal information, but were based primarily on plumage and external structural characters, led to conclusions that have not been accepted by the Neotropical ornithological community (Fitzpatrick 1982, Sibley & Monroe 1990, Ridgely & Tudor 1994, Remsen 2003).

During a general avian inventory of San Luis National Park, in the cerrado of northern Paraguay (Robbins *et al.* 1999), just after dawn on 22 October 1996, MBR tape-recorded (MLNS 107157 [all abbreviations are listed in the Acknowledgements]) a furnariid that he presumed, based on voice, to be a *Syndactyla*. Upon collecting the singing bird's mate (Univ. of Kansas Natural History Museum [KUNHM] 88363), MBR was surprised to discover that it was a *Philydor dimidiatum*. In addition to its *Syndactyla*-like voice, the bird had a slightly upturned mandible like other *Syndactyla*, and the plumage was reminiscent of *Syndactyla ruficollis*, a species long allocated to *Automolus* until vocal data led to its transfer to *Syndactyla* (Parker *et al.* 1985, Ridgely & Tudor 1994; see below).

Here we present vocal, plumage and morphological characters that lead us to hypothesise that *Philydor dimidiatum* is indeed more closely related to other *Syndactyla* than to taxa currently included in *Philydor*. Further, we comment on the possible close relationship of *dimidiatum* to *Simoxenops* and on the relationship between *Simoxenops* and *Syndactyla*. Based on limited sample sizes, it appears that within at least the Paraguayan *dimidiatum* population, sexual dichromatism is marked, an unusual trait in Furnariidae. Finally, we present information on habitat preferences, foraging, breeding and singing behaviour of this poorly known species.

Methods

We assume that vocalisations of foliage-gleaners, like those of other suboscines, are mostly or entirely inherited (Kroodsmas 1984, 1989, Kroodsmas & Konishi 1991), and consequently provide potentially informative characters for systematic study (Parker *et al.* 1995, Kratter & Parker 1997, Zimmer 1997, 2002, Remsen 2003). To analyse vocalisations, we assembled recordings of all but one, *Syndactyla guttulata*, of the currently recognised species of *Philydor*, *Syndactyla* and *Simoxenops*. Our personal recordings provided sufficient material for most species in these groups, but we supplemented these with material from other recordists, and, in two instances, from commercial compilations of bird recordings (see below). We excluded *Philydor novaesi* from consideration in our analysis, because certain aspects of its vocal repertoire are anomalous relative to all other members of the genus (KJZ unpubl.), and because our sample sizes were judged too small to support meaningful conclusions. We made auditory comparisons of all recordings and visual comparisons of spectrograms of each species for which representative recording samples were available. Vocalisations selected for illustration as spectrograms in this paper were deemed representative based on auditory comparison of the entire inventory, and on visual comparison of spectrograms of a smaller sample. Locations and recordists for all recordings examined are presented in Appendix 1.

We encourage readers to compare our descriptions of vocalisations with various commercially available sound compilations. The following collectively contain examples of vocalisations of many of the species involved in this study, and also will assist in interpreting the spectrograms: *Syndactyla rufosuperciliata* (Schulenberg 2000b); *S. subalaris* (Moore *et al.* 1999, Schulenberg 2000b); *Simoxenops striatus* (Schulenberg 2000a); *S. ucayalae* (Schulenberg *et al.* 2000); *Philydor rufum* (Moore *et al.* 1999); *P. fuscipenne* (Jahn *et al.* 2002, Moore *et al.* 2002); *P. erythrocerum* (Moore 1996, Schulenberg 2000a, Schulenberg *et al.* 2000); *P. pyrrhodes* (Moore 1996, Schulenberg *et al.* 2000); *P. erythropterum* (Moore 1996, 1997, Schulenberg *et al.* 2000); *P. ruficaudatum* (Schulenberg *et al.* 2000). Note that recordings from these sources are not included in our inventory, although the recordings of *Simoxenops striatus* (T. A. Parker recording; Schulenberg 2000a) and *Philydor fuscipennis* (M. Lysinger recordings; Moore *et al.* 2002) were consulted for want of other material.

For comparison, vocalisations were categorised as loudsongs or calls. Loudsongs were consistently patterned multi-note vocalisations (Isler *et al.* 1997), given seemingly in the context of territorial advertisement. Vocalisations characterised as calls usually were structurally simple (typically involving well-spaced repetition of identical notes or pairs of notes). These were given most frequently in the context of contact notes between mates, or as aggression calls during territorial conflicts with conspecifics, or in response to playback. Exceptions are noted in the results below. Our recordings were made with Sony TC D5 Pro-II

and Sony TCM-5000 recorders and Sennheiser ME-67, ME-80 and MKH-70 shotgun microphones. Spectrograms used in illustrations were made by P. R. Isler on a Macintosh G4 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York), Canvas graphics software (version 5.0.3, Deneba Software, Miami, Florida) and a Hewlett Packard Laserjet 6MP printer.

Dimidiatum specimens examined: Paraguay: two adult females and adult male, San Luis National Park (KUNHM 88362–3, Museo Nacional de Historia Natural del Paraguay, MNHNP); adult male, Apa Mts., Zanja Moroti (ZSM 32.814); adult male, Apa Mts., San Luis de la Sierra (ZSM 32.815). Brazil: *baeri* from Goiás (FMNH 75118, LACMNH 39956–7); adult female IBGE Reserve in Brasília, Distrito Federal (BMNH 1984.1.6); adult male and immature male, western Minas Gerais, Agua Suja at Bagagem (ZSM 1911.83; holotypes); adult male, Patrocínio, Minas Gerais (MNRJ 32973); adult male, Reserva Biológica do IBGE, Distrito Federal (MNRJ 33235); adult male, Nova Ponte, Minas Gerais (DZUFMG 707); an unsexed individual and adult female, Campo Alegre (between Serro and Minas Novas), Minas Gerais (DZUFMG 708–09); adult male Porto Camargo, Paraná (MZUSP 36872); adult female and immature male, Sangrador, Mato Grosso (NMW 16.359–60); immature male, rio Manso, Mato Grosso (NMW 19.353); adult male, Fazenda Recreio, Coxim, Mato Grosso (MZUSP 17258); male?, Sant'Anna do Parnaíba, Mato Grosso (MZUSP 12748).

Behavioural and habitat data are from field work conducted by MBR in 1996–97 (northern Paraguay), and by KJZ in 2002 and 2004 (Distrito Federal, Brazil), supplemented by observations made by A. Whittaker in 1996 in Minas Gerais, Brazil. All measurements used in behavioural data (distances, heights, etc.) are estimates.

Results

Vocalisations

The loudsong of *P. dimidiatum* (Figs. 1a–d, 1g) is a slow rattle with a distinctly nasal quality. It typically consists of a stuttering prelude or preamble of lower amplitude notes that accelerates into a higher amplitude series of fairly evenly paced and strident, nasal notes that may rise and fall somewhat in frequency (5–8 kHz) before accelerating toward the finale. The nasal notes can be distinguished in the spectrograms (Figs. 1a–d) by their difference in width relative to the introductory and terminal notes. The loudsongs vary greatly, both among individuals and from one song to the next within the same individual. Songs may vary greatly in overall length, and particularly in the presence or absence of a preamble, its length, and the extent to which it stutters (versus being evenly paced). These differences appear to be exacerbated by tape playback, and depending on the degree of agitation, the differences within a single individual's songs can be marked. Some of the observed variation may be the result of sexual differences. KJZ tape-recorded what appeared to be a mated pair in Brasília National Park

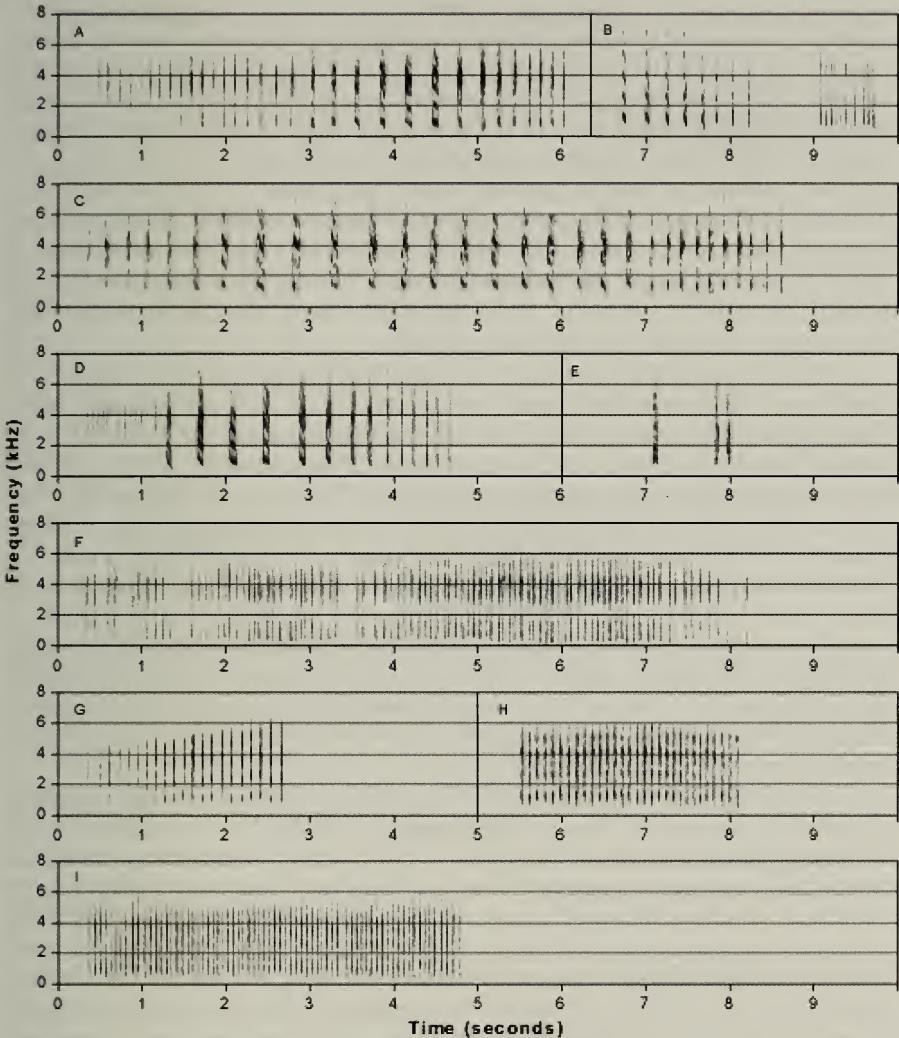


Figure 1. Vocalisations of *Philydor dimidiatum*. (a) natural song, from Brasília National Park, Distrito Federal, Brazil (21 August 2002; K. J. Zimmer). (b) different individual; short song, followed by rattle call, Brasília National Park, Distrito Federal, Brazil (20 August 2002; K. J. Zimmer). (c) responsive song of male-female duet, Brasília National Park, Distrito Federal, Brazil (21 August 2002; K. J. Zimmer). (d) initiating song of male-female duet, Brasília National Park, Distrito Federal, Brazil (21 August 2002; K. J. Zimmer). (e) call notes, Brasília National Park, Distrito Federal, Brazil (20 August 2002; K. J. Zimmer). (f) one rattle call, response to playback, Brasília National Park, Distrito Federal, Brazil (21 August, 2002; K. J. Zimmer). (g) natural song, San Luis National Park, Paraguay (22 October 1996; M. B. Robbins; MLNS 120469). (h) rattle call in response to playback, San Luis National Park, Paraguay (27 October 1996; M. B. Robbins; MLNS 120470). (i) rattle call in response to playback, Patas de Minas, Minas Gerais, Brazil (27 December 1996; A. Whittaker). All spectrograms by P. R. Isler.

(Distrito Federal, Brazil) that sang repeated duets, in which one bird consistently initiated the duet, and the other delivered its song in a responsorial fashion, usually immediately after the termination of the initiating bird's song. The song of the bird that initiated the duets (Fig. 1d; the presumed male, although this could not be verified) was usually preceded by a low-amplitude preamble and contained roughly half the number of high-amplitude, nasal notes as the song of the responding bird (Fig. 1c), the song of which typically lacked any preamble. The few loudsongs recorded in Paraguay (Fig. 1g) sound generally similar to those from central Brazil in pattern, although distinctly less nasal in quality, as evidenced by the lack of change in note-shape over the course of the song. The significance of this apparent difference is difficult to assess given the small sample size of loudsongs from Paraguay and individual variation as noted above.

Apart from loudsongs, two other types of vocalisations were recorded from *P. dimidiatum*. One was a single-noted or doubled *TCHACK* or *TCHEK* (6–7 kHz), with a harsh, slightly nasal quality (Fig. 1e). These calls were given as contact notes between members of pairs that were separated whilst foraging. They were also given as aggression calls in response to playback. The other vocalisation type was a somewhat harsh-sounding rattle, generally evenly paced and of fairly uniform frequency (c.6 kHz), but varying greatly in length (1–10 seconds) (Figs. 1f, 1h, 1i). As noted with loudsongs, variation in the length of rattle calls appeared to be as great within individuals as among individuals, and was particularly susceptible to the influence of playback. Rattle calls were often given immediately before or after loudsongs, but were also given as antagonistic calls in response to the vocalisations of a neighbouring conspecific or to playback. Birds responding to playback consistently gave longer rattles. Rattle calls from Paraguay (Fig. 1h) sounded similar to those from Brazil (Figs. 1b, 1f, 1i).

Our inventory of recordings included vocalisations of three of the four currently recognised species of *Syndactyla* (*subalaris*, *ruficollis*, *rufosuperciliata*). Loudsongs of these three species (Figs. 2a, 2c, 2e) were remarkably similar in pattern and quality, and consisted of a series of nasal, chattering notes (1.5–3.5 seconds in duration, delivered at c.6–8 kHz) that usually accelerated markedly toward the end and often ended abruptly. The terminal, more closely spaced notes were less nasal in quality compared to the introductory and middle notes of the song, as evidenced by the difference in note-width. As with *P. dimidiatum*, songs of the three *Syndactyla* species varied greatly in length, frequency shifts and pace changes (acceleration or deceleration within the song), both among individuals in a population and from one song to the next from the same individual, and were influenced by playback and degree of agitation of the responding bird. Calls of the three *Syndactyla* species (Figs. 2b, 2d, 2f) were also remarkably uniform between species, consisting of a harsh, nasal *TCHEK*, *TCHECH* or *TCHAK* (6–8 kHz).

Loudsongs of *Simoxenops ucayalae* resembled those of *P. dimidiatum* and the three *Syndactyla* species in being a long series of closely spaced, harsh notes, with a distinctly nasal quality (Figs. 2g,h) They were lower in frequency (c.3–4 kHz)

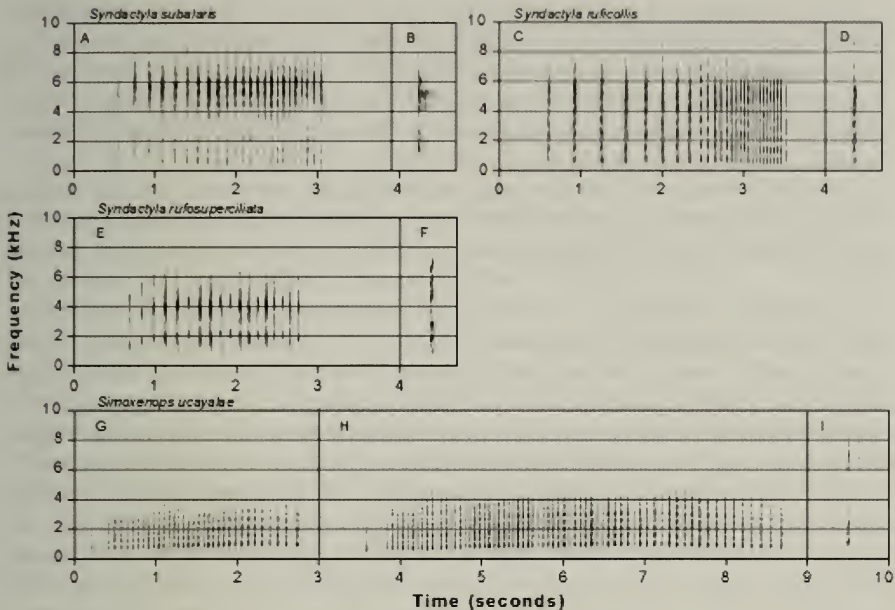


Figure 2. Vocalisations of various species of *Syndactyla* and *Simoxenops* foliage-gleaners. (a) *Syndactyla subalaris*: natural song, Monteverde Cloud Forest Reserve, Costa Rica (March 1994). (b) *Syndactyla subalaris*: single-note call, Cerro de la Muerte, Costa Rica (March 1997). (c) *Syndactyla ruficollis*: natural song, Abra Porculla, dpto. Piura, Peru (24 January 2001). (d) *Syndactyla ruficollis*: single-note call, Abra Porculla, dpto. Piura, Peru (24 January 2001). (e) *Syndactyla rufosuperciliata*: natural song, Serra do Caraça, Minas Gerais, Brazil (6 September 2001). (f) *Syndactyla rufosuperciliata*: single-note call, Itatiaia National Park, Rio de Janeiro, Brazil (21 October 1998). (g) *Simoxenops ucayalae*: natural song, Serra dos Carajás, Pará, Brazil (9 February 2003). (h) *Simoxenops ucayalae*: long song in response to playback, Alta Floresta, Mato Grosso, Brazil (25 August 1991). (i) *Simoxenops ucayalae*: single-note call, Alta Floresta, Mato Grosso, Brazil (25 August 1991). All recordings by K. J. Zimmer. All spectrograms by P. R. Isler.

than the loudsongs of *P. dimidiatum* or *Syndactyla*, but varied similarly in overall song-length (*c.* 3–5 seconds), frequency shifts and in changes of pace (acceleration and deceleration) between songs from the same individual. Like *P. dimidiatum* and the *Syndactyla* species, this variation was subject to influence by playback and the degree of agitation of the responding bird. In contrast to the three *Syndactyla* species, the loudsongs of *Simoxenops ucayalae* typically accelerated more markedly over the first part of the song and slowed at the end, but still ended abruptly. In this respect, they were more similar to loudsongs of *P. dimidiatum*, which often commenced with a preamble of closely spaced notes that then slowed to the main series of more widely spaced nasal notes. Loudsongs of *S. ucayalae* were also similar to those of *P. dimidiatum* in often beginning with a stuttering start

of lower frequency and lower amplitude notes. Our inventory contained only a single recording of *Simoxenops striatus*, and this precludes generalisations concerning its vocalisations. However, loudsongs of the single *striatus* were similar to those of *ucayalae* in pattern and quality. The call of *S. ucayalae* is a harsh, nasal TCHAK (Fig. 2i), similar to that of *P. dimidiatum* and the three *Syndactyla* species surveyed.

The eight species of *Philydor* analysed (excluding *dimidiatum*) can be divided into three vocal groups based on differences in loudsongs. The first group consists of *P. lichtensteini* and *P. erythrocercum*. Loudsongs of these species (Figs. 3a, 3d) consist of a countable series of distinctly spaced, sharp or squeaky notes. The second group includes *P. atricapillus*, *P. erythropterum* and *P. pyrrhodes*. Loudsongs in this group (Figs. 3b, 3c, 3e) consist of a long series of uncountable, closely spaced notes that form a trill. In general, these songs show relatively slight changes in frequency from start to finish, although that of *P. pyrrhodes* is distinguished by a distinct change in amplitude commencing with the middle third of the song (Fig. 3e). The third group includes *P. rufum*, *P. ruficaudatum* and *P. fuscipenne*. Loudsongs of these species (Fig. 3f) are somewhat intermediate (relative to the other two groups) with respect to the number of notes and the spacing. They could be characterised as rattles that change in pace or frequency (sometimes several times) over the course of the song, and that have a more 'staccato' or 'ratchety' quality. None of the eight species considered here has a loudsong whose notes could be characterised as imparting (either individually or in entirety) a 'nasal' quality. In marked contrast to *P. dimidiatum*, the various *Syndactyla* species and *Simoxenops ucayalae*, none of the eight species of *Philydor* shows any tendency for marked intra-population variation in song characters, either between or within individuals. Also in contrast to *P. dimidiatum*, *Syndactyla* and *Simoxenops ucayalae*, *Philydor* species do not conspicuously alter the length or other aspects of their loudsongs in response to playback. However, in response to playback, *P. pyrrhodes* does regularly give a long, low-amplitude rattle call similar to the loudsong but without shifts in amplitude, pace or frequency (KJZ unpubl.).

Calls of the eight *Philydor* species (excluding *dimidiatum* and *novaesi*) show no unifying threads, and vary considerably from one species to the next. Calls from our inventory are as follows: (a) *erythrocercum*—an explosive, somewhat squeaky SQUEET! or an ascending, loud WHEEEK!; (b) *ruficaudatum*—a thin, brittle rattle tsissiiitt with the quality of a waxwing (*Bombycilla*); (c) *fuscipenne*—a thin, sharp cheet or steet, and a short, staccato chidideet; (d) *rufum*—a hard JIK!; (e) *atricapillus*—a squealing, loud SKEW or SPREE, and a loud series of 3–4 ascending whistled TWEEET notes; (f) *lichtensteini*—a thin, abbreviated fast rattle skit't'r'r'r't; (g) *erythropterum*—a shrill KREEEAH or KREER; (h) *pyrrhodes*—a hard chidit or chikit and, in response to playback, a prolonged, low-amplitude rattle (sometimes lasting up to 30 seconds).

Behaviour

In northern Paraguay and in Minas Gerais, Brazil (A. Whittaker, G. M. Kirwan pers. comms.), presumed pairs were observed singing and foraging solitarily, once in association with a mixed-species flock, at c.4–12 m above ground in the dense vine tangle-dominated understorey of semi-humid forest. Birds were observed hitching up vines and small saplings as they foraged. Whittaker observed a foliage-gleaner capture a centipede and remove its exoskeleton before swallowing it. Following playback, males responded by approaching and counter-singing from perches within dense vegetation. When counter-singing, the head was held upward at c.45° and the wings and tail vibrated.

At Brasília (Distrito Federal, Brazil), pairs of *P. dimidiatum* occupied semi-humid gallery forest. Members of presumed mated pairs foraged mostly in fairly close association, maintaining contact through regular vocalisations. They foraged 1.5–12.0 m above ground, but primarily at 3–7 m, hitching through woody vine tangles or along more open limbs. Foraging birds regularly flicked both wings simultaneously, a movement that was usually accompanied by a simultaneous shallow vertical flick of the tail. Arthropod prey was mostly gleaned from branch or vine surfaces by reaching, followed by a quick stab of the bill. Acrobatic manoeuvres, such as hanging, were occasionally employed, and birds regularly used their bill to hammer at loose bark, stems or dead leaves, sometimes probing into arboreal leaf litter suspended in vines. KJZ videotaped one individual that seized a small dead twig with its bill, broke it off at the base, then used its foot to secure the twig while repeatedly hammering and probing in the fractured end of the twig with its bill, much in the manner of a *Xenops*. On one occasion, a pair of *dimidiatum* foraged in loose association with a mixed-species flock of insectivores; all other observations of the species from Brasília were of solitary pairs or individuals.

Morphology

The recent collection of two females from Paraguay reveals that sexual dichromatism is marked in *P. dimidiatum*, at least in the Paraguayan population (Fig. 4). The adult female specimens (KUNHM 88362–3) are distinct ventrally from the adult male (deposited at MNHNP; MLNS 107158; presumed mate of KUNHM 88362) taken at the same site and from two adult males taken within 75 km (ZSM 32.814, 32.815). The chin and centre of the throat of each of the two females are pale buffy-white contrasting with the cinnamon-rufous throat-sides and malar region. The centre of each breast and abdominal feather is ochraceous, contrasting with the remainder of the feather, which is tinged cinnamon-rufous. The ochraceous shafts are particularly conspicuous on the brownish-olive flank feathers (Fig. 4). As stated earlier, this pattern gives the underparts an indistinctly flammulated appearance, somewhat like those of *Syndactyla ruficollis* (see Ridgely & Tudor 1994: pl. 9). Flammulations on the underparts are less conspicuous in Paraguayan males, in which the ventral surface matches that of specimens from

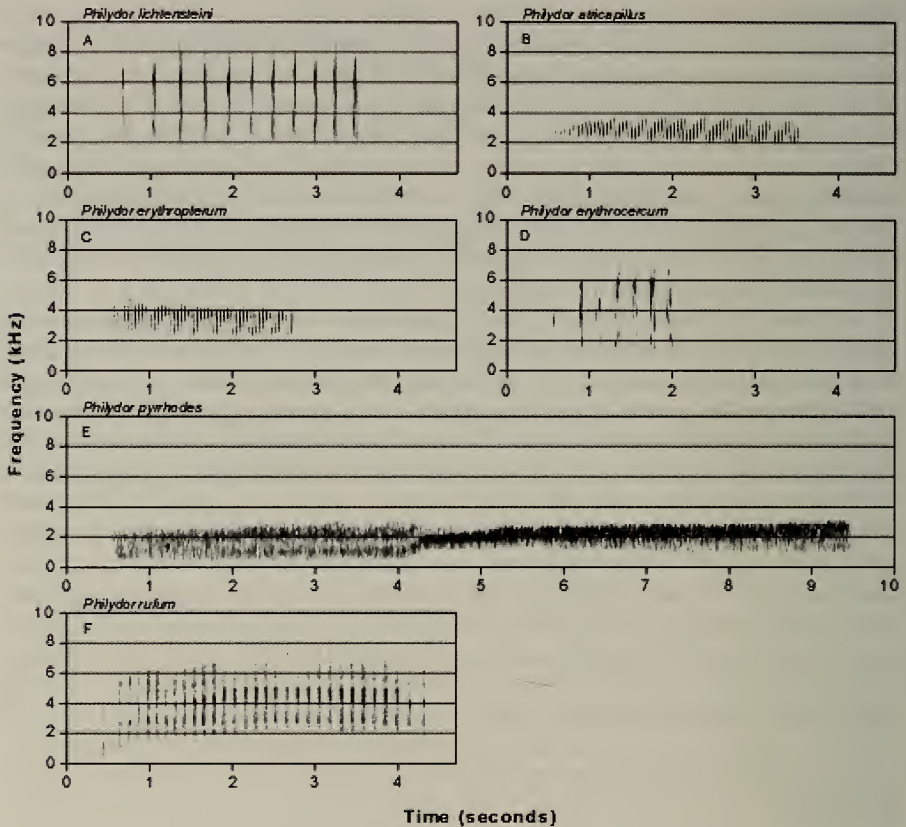


Figure 3. Vocalisations of various species of *Philydor* foliage-gleaners. (a) *P. lichtensteini*: song, response to playback, Iguaçu National Park, Paraná, Brazil (12 October 1999). (b) *Philydor atricapillus*: song, response to playback, Iguaçu National Park, Paraná, Brazil (23 September 2002). (c) *Philydor erythropterum*: natural song, Manu Wildlife Center, dpto. Madre de Dios, Peru (5 August 2000). (d) *Philydor erythrocerum*: song in response to playback, Caxiuanã, Pará, Brazil (3 August 2001). (e) *Philydor pyrholdes*: natural song, Tambopata Research Center, dpto. Madre de Dios, Peru (19 August 1994). (f) *Philydor rufum*: natural song, Itatiaia National Park, Rio de Janeiro, Brazil (18 October 2000). All recordings by K. J. Zimmer. All spectrograms by P. R. Isler.

throughout the known distribution of the species. The only other females are of an apparent adult taken in Brasília, Distrito Federal (BMNH 1984.1.6), an adult female from Sangrador, Mato Grosso (NMW 16.359) and another, apparently adult, taken at Campo Alegre, Minas Gerais (DZUFMG 709). At least one bird videotaped by KJZ in Brasília had vaguely flammulated underparts similar to those of the females collected in Paraguay; the underparts of the other individual videotaped could not be seen well enough to permit comparison of this feature.

The following data from KUNHM, one MNRJ and the BMNH specimens are the first published mass and soft-part coloration data for the species: both females 31 g, two males 29 g and the other (MNRJ 33235) 31 g; none exhibited fat nor any moult. Irides brown (very dark chestnut in MNRJ 33235), maxilla dark brown, mandible pale grey or horn (described as greenish horn for MNRJ 33235), with a pinkish base, and tarsi olive or greenish. Based on vocalisations and gonad size, this species was breeding at the San Luis site in late-October 1996, as were many other avian species (Robbins *et al.* 1999). The male's largest testis was 12 × 6.5 mm and both females had recently laid, as they had convoluted oviducts 4 mm in diameter. One female had a completely ossified skull and the other's was 50% ossified, but neither had a bursa of Fabricius. Other specimen data are: one male from Brazil (MNRJ 33235), taken in early November, had testes of 7 × 5 mm, and the female taken in Minas Gerais, Brazil, had an oviduct of 5 × 3 mm in mid June. Pairs of *dimidiatum* at Brasília were vocal and territorial in August 2002, suggesting breeding during that time. At the same spot in February 2004, they were silent and unresponsive to playback, suggesting a lack of breeding activity. In Minas Gerais the species appears to be most vocal (and responsive to playback) in September to January, which would accord with the general breeding season for birds in this region (G. M. Kirwan pers. comm.).

Discussion

Philydor dimidiatum is one of the most poorly known birds in the Western Hemisphere; we located only 20 museum specimens and only 12 of those had additional data beyond locality and collection date. Only five of the 20, all collected relatively recently, were females. Presumably, the combination of small sample sizes and the lack of modern data has led to some confusion concerning distribution and plumage. As currently treated (Remsen 2003), *P. dimidiatum* consists of two subspecies: nominate *dimidiatum* and *baeri*. Peters (1951) outlined nominate *dimidiatum* as restricted to southern Mato Grosso, with *baeri* in Minas Gerais and Goiás, Brazil, and in north-east Paraguay. However, Ridgely & Tudor (1994) attributed Paraguayan birds to the nominate race. Direct comparison of the adult male *baeri* holotype with the two adult male Paraguayan specimens at ZSM demonstrated that the birds are virtually indistinguishable. When Hellmayr (1925) described *baeri* he characterised it as being overall less rufescent, especially on the dorsum, than nominate. Comparison of digital photos of the holotypes suggests that the nominate form is indeed more rufescent, at least dorsally, than *baeri*, but additional material from Mato Grosso is needed to confirm this.

What is clear from the recent collection of two females is that there is marked sexual dichromatism in at least the Paraguayan population. Within the Furnariidae very few species exhibit sexual dichromatism and all examples are subtle (Remsen 2003). Thus, the rather marked sexual differences in the amount of flammulation on the underparts of this foliage-gleaner appear to represent the extreme example of

sexual dichromatism in the family. Larger sample sizes are needed to ascertain whether females are significantly smaller than males in wing and tail length.

Generic relationships of the many foliage-gleaners comprising the philydorine assemblage have long been disputed. Vaurie (1980) recommended an expanded concept of the genus *Philydor* that included, among many others, the currently recognised genera *Syndactyla* and *Simoxenops*. Although Vaurie's views failed to gain wide acceptance, the generic placement of some foliage-gleaners has shifted between *Syndactyla* and other genera, suggesting that characters used to separate these genera are not well defined. The taxon *Syndactyla mirandae* was described from Goiás, Brazil, and for a time was treated as a subspecies of *S. rufosuperciliata* before it was determined to be a synonym of *P. dimidiatum* (Remsen 2003). More recently, *Syndactyla ruficollis*, although divergent in plumage characters from the three recognised species of *Syndactyla*, was transferred to that genus from



Figure 4. Ventral view of male and female *Philydor dimidiatum*. Left to right: female, KUNHM 88362; male, LACM 39956; female, KUNHM 88363; male, LACM 39957. See text for locality information. Note more pronounced flammulations on females.

Automolus, based largely on striking similarities in vocal characters (Parker *et al.* 1985, Ridgely & Tudor 1994).

Chapman (1928) erected the genus *Anachilus* (subsequently recognised as preoccupied; Chapman 1937) in describing a distinctive new furnariid from the upper río Ucayalae, Peru. In erecting *Anachilus* (= *Simoxenops*) for *ucayalae*, Chapman emphasised the large size, uniformly rufescent coloration and uniquely shaped bill as distinguishing characters. It is unlikely that Chapman compared *ucayalae* to *P. dimidiatum*, given the latter's rarity in collections. The only other member of the genus, *Anachilus* (*Simoxenops*) *striatus*, was described by Carriker (1935). He provided no specific rationale for considering it to be congeneric with *ucayalae*, commenting mainly that *striatus* was easily separated from *ucayalae* by the presence of distinct streaking on the crown, nape, mantle and chest. He also noted that the bill of *striatus* was shorter than that of *ucayalae*, and that the habits of the bird were 'much like those of *Philydor*'.

Like all *Syndactyla*, and both species of *Simoxenops*, *P. dimidiatum* has a distinctly upturned mandible, or 'ascending gonys' (Vaurie 1980, Remsen 2003). Within currently recognised *Syndactyla*, trans-Andean *ruficollis* is most similar in plumage characters to *P. dimidiatum*, both species being largely unstreaked compared to other *Syndactyla*. If *dimidiatum* were to be transferred to *Syndactyla*, then the plumage and morphological distinctions between *Syndactyla* and *Simoxenops* become even less pronounced. From a plumage perspective, nominate *dimidiatum* appears to be just a smaller version of *Simoxenops ucayalae*. Both species are rufescent in overall coloration, lack streaking, and have a pale supercilium and distinctly upturned mandible. Further blurring differences between *Simoxenops* and *Syndactyla* is that *Simoxenops striatus* is roughly intermediate in overall size and bill size between *S. ucayalae* and *Syndactyla*, and the plumage of *striatus* is as similar to *Syndactyla ruficollis* as it is to *Simoxenops ucayalae* (Remsen 2003, J. V. Remsen pers. comm.). Thus, if *Syndactyla*, *P. dimidiatum* and *Simoxenops* are considered collectively, there is a gradient in plumage and structure from the smaller billed, heavily streaked *Syndactyla* to the larger billed, unstreaked *Simoxenops ucayalae*. The extreme bill size and shape of *ucayalae*, upon which *Simoxenops* is largely based, is probably an evolutionary response to foraging specialisation on *Guadua* bamboo (Remsen 2003), and is bridged by *Simoxenops striatus* to *Syndactyla*, which shares a similarly shaped but smaller bill. *P. dimidiatum*, *Simoxenops striatus* and *Syndactyla ruficollis* similarly bridge the gap in plumage characters between the unstreaked *ucayalae* and the heavily streaked *Syndactyla*.

Vocal characters may provide the strongest argument for the relatedness of *dimidiatum* to *Syndactyla* and *Simoxenops*, and for the separation of these species from the currently recognised *Philydor*. Loudsongs of the three *Syndactyla* species represented in our inventory were remarkably uniform in pattern and note quality. Calls of these species were also strikingly similar to one another. Indeed, the vocalisations of all three species are so similar that they are easily confused by the

uninitiated listener. All are united by the harsh, nasal quality of their notes (both in loudsongs and in calls), the accelerating pattern of the loudsong, the often stuttering start to the loudsong, and the variation in loudsong length, changes of pace and frequency shifts displayed by individuals, particularly in response to playback. In describing vocalisations of the various members of the genus, Ridgely & Tudor (1994) employed 'a distinctive accelerating series of harsh nasal notes, stuttering at first' for *subalaris*, and 'a series of harsh, nasal, ratchety notes which starts slowly and then speed up' for *ruficollis*. Although the fourth currently recognised species in the genus, *S. guttulata*, was not represented in our sample, published descriptions of its vocalisations are consistent with those of the other members of the genus. Hilty (2003) described the song of *guttulata* as 'a harsh, accelerating 'cjak, cjak, cjak, cjak-zak-zak-zak-za-za-za'', sometimes followed by a few more notes', and the call as 'a harsh, rough 'chak''. Ridgely & Tudor (1994) likened the vocalisations of *guttulata* to those of *subalaris*.

The vocalisations of *P. dimidiatum* are strikingly similar to those of the four other *Syndactyla*. They have the same harsh, nasal quality to the calls and to the individual and collective notes of the loudsongs. The loudsongs typically commence with a stuttering preamble, and they show much variation in length, pace changes and frequency shifts from one song to the next in the same individual. These vocal characters are shared by both *Simoxenops*. The vocal similarities between *Simoxenops* and *Syndactyla* were first noted by Parker (1982), and have been echoed by subsequent authors (Parker & Bates 1992, Ridgely & Tudor 1994, Remsen 2003).

Conversely, the vocalisations (particularly the loudsongs) of *P. dimidiatum* are not noticeably similar to those of any of the other recognised species of *Philydor*, none of which shares the distinctive nasal quality that immediately distinguishes *dimidiatum*, *Syndactyla* and *Simoxenops*. More important, perhaps, is that our samples of other *Philydor* species (with the exception of *P. pyrrhodes*) showed no evidence of the capacity for individual variation in songs and calls that typifies *P. dimidiatum*, a seemingly ubiquitous feature of vocalisations of the various species of *Syndactyla* and *Simoxenops*. The other *Philydor* species respond to playback by giving songs and calls indistinguishable from natural (unsolicited) vocalisations, whereas *dimidiatum*, *Syndactyla* and *Simoxenops* display complex repertoires that involve numerous permutations of the natural vocalisations depending on their overall degree of agitation. Also in contrast to *Syndactyla* and *Simoxenops*, the genus *Philydor* does not display great uniformity in loudsongs, and almost none in calls.

In all of its vocal characters and in its distinctly upturned mandible, *P. dimidiatum* is much more like all of the currently recognised species of *Syndactyla* than any currently recognised species of *Philydor*. In plumage characters, it is closest to *Simoxenops ucayalae*, but is also similar to *Syndactyla ruficollis* in having some flammulation on the underparts but lacking true streaking. Moreover, behaviourally, *dimidiatum* is also a closer fit with *Syndactyla* and *Simoxenops* in

gleaning primarily from branch or vine surfaces, employing hammering or chiseling motions of the bill, and in often foraging apart from mixed-species flocks. The hammering or chiseling of substrates has been noted for *S. guttulata*, *S. rufosuperciliata* (Remsen 2003) and *S. ruficollis* (KJZ unpubl.), and is a primary search manoeuvre of both species of *Simoxenops* (Parker 1982, Remsen & Robinson 1988, Parker & Bates 1992, Kratter & Parker 1997, Zimmer *et al.* 1997). Conversely, this behaviour is rare (at best) or absent in *Philydor*, most species of which are dead-leaf specialists (Remsen 2003). Although all *Syndactyla* species regularly associate with mixed-species flocks, they are less habitual in their attendance than are *Philydor*, most of which are inveterate members of such flocks, and are rarely encountered away from them (pers. obs.; Remsen 2003).

Taxonomic recommendation

We recommend that '*Philydor*' *dimidiatum* be placed in the genus *Syndactyla*; the name would thus become *Syndactyla dimidiatum* (Pelzeln). Based on plumage, structural and vocal characters we also recommend that *Simoxenops* be subsumed in *Syndactyla*, which has priority. In a linear sequence *dimidiatum* should be placed between *S. ruficollis* and *Syndactyla* [*Simoxenops*] *ucayalae*. This change dictates that two scientific names be modified if *Simoxenops* is subsumed within *Syndactyla* and *dimidiatum* transferred to the latter: *Philydor dimidiatum* becomes *Syndactyla dimidiata*, and *Simoxenops striatus* becomes *Syndactyla striata*, as both specific names are variable adjectives in a new combination with a feminine genus (S. M. S. Gregory *in litt.* 2004, N. David *in litt.* 2004). A molecular-based phylogeny is required to confirm our hypotheses and to clarify relationships within the now more inclusive *Syndactyla*.

As far as is known, only birds from the type locality possess a 'russet' dorsum; over the rest of the range the dorsum is olive-brown, thus we find Ridgely & Tudor's recommendation of applying the English name Planalto Foliage-gleaner to be more appropriate than Russet-backed Foliage-gleaner.

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APPENDIX

Recording locations and recordists. Numbers following each name represent the number of individual birds recorded by the recordist at each site.

- Philydor dimidiatum*.—BRAZIL: Brasília National Park, Distrito Federal (K. J. Zimmer, 5); Patas de Minas, Minas Gerais (A. Whittaker, 1). PARAGUAY: San Luis National Park (M. B. Robbins, 2, MLNS 120469–70).
- Philydor ruficaudatum*.—BRAZIL: Serra dos Carajás, Pará (K. J. Zimmer, 4); Alta Floresta, Mato Grosso (K. J. Zimmer, 2).
- Philydor erythrocercum*.—BRAZIL: Caxiuanã Forest Reserve, Pará (K. J. Zimmer, 3); Fazenda Rancho Grande, Rondônia (K. J. Zimmer, 1); rio Cristalino, Alta Floresta region, Mato Grosso (K. J. Zimmer, 3); rio Mapiá, Borba region, Amazonas (K. J. Zimmer, 1); Serra dos Carajás, Pará (K. J. Zimmer, 2). ECUADOR: Tiputini Biodiversity Station, Napo (K. J. Zimmer, 1).
- Philydor erythropterum*.—BRAZIL: Fazenda Rancho Grande, Rondônia (K. J. Zimmer, 3). ECUADOR: Tiputini Biodiversity Station, Napo (K. J. Zimmer, 3). PERU: Manu Wildlife Center, dpto. Madre de Dios (K. J. Zimmer, 1).
- Philydor lichtensteini*.—BRAZIL: Iguaçu National Park, Paraná (K. J. Zimmer, 25); Volta Velha Reserve, Santa Catarina (K. J. Zimmer, 3). PARAGUAY: dptos. Caazapá and Concepción (M. B. Robbins, 7; MLNS 120472–7).
- Philydor atricapillus*.—BRAZIL: Garuva, Paraná (K. J. Zimmer, 1); Iguaçu National Park, Paraná (K. J. Zimmer, 6); Ubatuba region, São Paulo (K. J. Zimmer, 5); Volta Velha Reserve, Santa Catarina (K. J. Zimmer, 2). PARAGUAY: dpto. Caazapá (M. B. Robbins; MLNS 120471).
- Philydor rufum*.—BRAZIL: Itatiaia National Park, Rio de Janeiro (K. J. Zimmer, 12); Augusto Ruschi Reserve, Espírito Santo (K. J. Zimmer, 1). PERU: Manu Wildlife Center, dpto. Madre de Dios (K. J. Zimmer, 1); Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 1).
- Philydor pyrrhodes*.—BRAZIL: rio Cristalino, Alta Floresta region, Mato Grosso (K. J. Zimmer, 1). PERU: Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 1). VENEZUELA: Yapacana National Park, Amazonas (K. J. Zimmer 1). GUYANA: (M. B. Robbins, 3; MLNS 120478–80).
- Syndactyla subalaris*.—COSTA RICA: Cerro de la Muerte (K. J. Zimmer, 1); Monteverde Cloud Forest Reserve (K. J. Zimmer, 10); Tapanti Faunal Reserve (K. J. Zimmer, 1). PANAMA: Chiriquí (M. B.

Robbins, 2; MLNS 120481-2). PERU: Abra Patricia, dpto. San Martín (K. J. Zimmer, 1). ECUADOR: prov. Morona-Santiago (M. B. Robbins, 2; MLNS 41285 & 41287).

Syndactyla rufosuperciliata.—BRAZIL: Itatiaia National Park, Rio de Janeiro (K. J. Zimmer, 13); Fazenda Pindobas IV, Espírito Santo (K. J. Zimmer, 2); São Francisco de Paula region, Rio Grande do Sul (K. J. Zimmer, 10); Serra do Caraça, Minas Gerais (K. J. Zimmer, 3); Serra da Graciosa, Paraná (K. J. Zimmer, 1). PERU: Cosñipata Road, dpto. Cusco (K. J. Zimmer, 2). PARAGUAY: dpto. Caazapá (M. B. Robbins, MLNS 120483).

Syndactyla ruficollis.—PERU: Abra Porculla, dpto. Piura (K. J. Zimmer, 6); Tumbes Reserved Zone, dpto. Tumbes (K. J. Zimmer, 1); ECUADOR: prov. Loja (M. B. Robbins, 1; MLNS 57080).

Simoxenops ucayalae.—BRAZIL: Alta Floresta, Mato Grosso (K. J. Zimmer, 3); rio Cristalino, Alta Floresta region, Mato Grosso (K. J. Zimmer, 4); Serra dos Carajás, Pará (K. J. Zimmer, 4). PERU: Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 2).

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Some taxonomic comments on the genus *Polyplectron* (Phasianidae)

by John Penhallurick & Michael Walters

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An instance of possible priority arises in relation to one of the subspecies of Grey Peacock-pheasant *Polyplectron bicalcaratum* (Linnaeus, 1758), namely *P. b. bakeri* Lowe, 1925. The type locality of Lowe's name is 'Bhutan Doars', and the current distribution of the race is north-east India, in Sikkim, Assam, Arunachal Pradesh and Bhutan. Several earlier names appear to have been available for this race when Lowe applied his name¹, specifically:

Polyplectron cyclospilum G. R. Gray, 1867. *List of the specimens of birds in the British Museum*, pt. 5, Gallinae, p. 23; and

Polyplectron enicospilum G. R. Gray, 1867. *List of the specimens of birds in the British Museum*, pt. 5, Gallinae, p. 24.

However, it appears that Lowe's separation racially of birds from north-east India and Bhutan was invalid. MPW compared skins at The Natural History Museum (NHM, Tring) of nominate *bicalcaratum* with the type of *bakeri* and could

¹ Anyone familiar with *Polyplectron hardwickii* J. E. Gray, 1830–32, *Illustrations of Indian zoology, chiefly selected from the collection of Maj.-Gen. Hardwicke*, 1: pl. 37, whose type locality is given as 'India' might wonder whether this name does not also predate Lowe's *bakeri*. However, examination of the plate makes it clear that this is an instance of *Polyplectron malacense* (Scopoli, 1786). Ogilvie-Grant (1893, *Catalogue of the birds of the British Museum* 22: 259) correctly gives the type locality of *P. hardwickii* and *P. lineatum* J. E. Gray, 1829, as 'Malacca' (the locality of the latter being given by Gray as 'China').